UCRL- 95054
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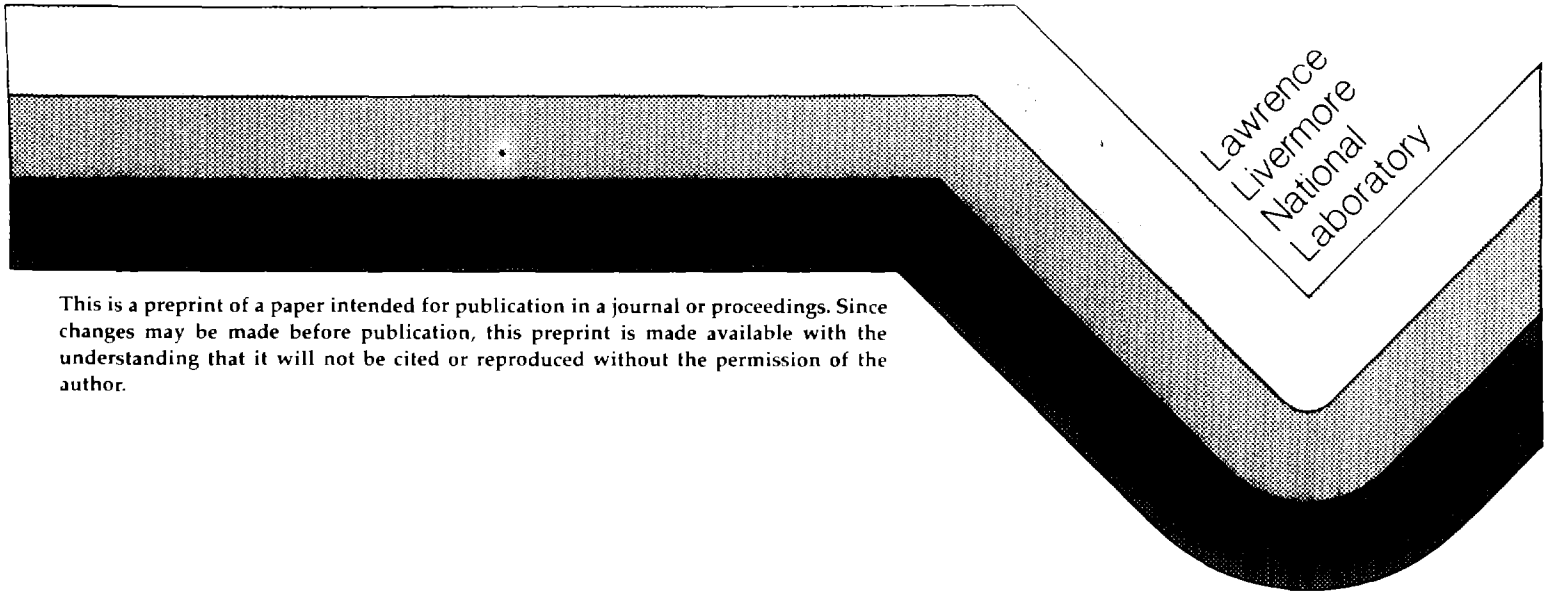
This paper was prepared for submittal to
North American Forest Biological Workshop
Society of American Foresters at Oklahoma State University
Stillwater, Oklahoma
June 16, 1986

June 1986



# GROWTH AND MORPHOLOGY OF PINUS PONDEROSA SEEDLINGS EXPOSED TO LONG-TERM ELEVATED ATMOSPHERIC CARBON DIOXIDE CONCENTRATIONS

James L.J. Houpis[1/], Kris A. Surano[2/], Paul F. Daley[2/], and Joseph H. Shinn[2/]

Abstract.--The growth and morpohology of two varieties of Pinus ponderosa were measured after two years of continuous fumigation with carbon dioxide. After two years of treatment, the seedlings of the Rocky Mountain variety showed no significant difference in total stem height or volume, but the basal diameters of those grown at +300ppm $CO_2$ were significantly greater than those grown at +0ppm and +75ppm. The response of the seedlings of the Sierran variety in these parameters was quite different, with those at +150ppm and +300ppm significantly greater in height than those at +75ppm, and those at +150ppm and +300ppm significantly greater than those at +0ppm and +75ppm in basal diameter and stem volume. However, using a combined analysis based on percent change in height, diameter, or volume, seedlings at +150ppm responded to a significantly greater degree than all other levels. Thus, the beneficial effects of elevated carbon dioxide increase up to +150ppm and begin to decrease between +150ppm and +300ppm.

Additional keywords: Ponderosa pine, Pinus ponderosa var ponderosa, Pinus ponderosa var scopulorum, carbon dioxide, biomass, $CO_2$ responses.

A long-term fumigation study of the effects of elevated atmospheric carbon dioxide on ponderosa pine (Pinus ponderosa) was conducted at the Lawrence Livermore National Laboratory, Livermore, California. Ponderosa pine was chosen because of its economic importance to the western United States and also because of the scarcity of long-term physiological and morphological studies of the effects of elevated carbon dioxide on long-lived woody species. This paper examines the growth and morphological responses of seedlings in the study. A related study in these proceedings by Fried et al. (1986) addresses nutrient and biomass responses of saplings.

## METHODS

Exposure with elevated carbon dioxide began in July 1983 and was terminated in September 1985. Exposures were continuous and were conducted in four standard open-top fumigation chambers as described by Heagle et al. (1973) and Rogers et al. (1983a, 1983b). The levels of carbon dioxide exposure were ambient (approximately 350ppm; +0ppm), ambient + 75ppm (+75ppm), ambient + 150ppm (+150ppm), and ambient + 300ppm (+300ppm).

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Work performed under the auspices of the U.S. Department of Energy by the Lawrence Livermore National Laboratory under contract W-7405-ENG-48. Mark P. Costella and Robert J. Palassou are acknowledged for their contribution to this study.

A monitoring system was developed to monitor and maintain these levels (Surano et al. 1986).

The experiments used seedlings of two varieties of ponderosa pine, one being the Sierran variety (P. ponderosa var ponderosa) and the other the Rocky Mountain variety (P. ponderosa var scopulorum). At the initiation of the fumigation, the Sierran variety was one-year old, and the Rocky Mountain variety was three-years old. Both varieties of seedlings were potted in 4L containers using a soil mixture containing equal parts of cohasset clay loam, redwood compost, #4 Monterey sand, and perlite. Throughout the study, all seedlings were maintained under well-watered conditions, fertilized regularly, and grown under shade. There were ten seedlings for each treatment.

Growth measurements were taken from April 1984 to August 1985. Basal diameter was determined using a micrometer placed at the cotyledon whorl. Two perpendicular measurements were taken and were averaged. Height measurements were taken from the cotyledon whorl to the top of the apical meristem using a tape measure. Volume was calculated from the diameter and height measurements using a parabolic formula (Husch et al. 1972).

Morphological data were collected at the conclusion of the exposure. Morphological measurements included biomass, volume, specific gravity, height, diameter, needle dry weight and surface area, and the number of buds. Biomass data included dry weight of main stem and lateral stems by age class, roots, needles, and buds. Specific gravity was calculated as the ratio of dry weight per volume of the main stem segment. Height and diameter measurements were taken for each stem segment. Finally, the amount of mid-needle abscission was observed as a percent of total needles present.

Statistical analysis was conducted using analysis of variance, but is not presented here. Comparisons among treatments were made using the Newman-Kuels Multiple Comparison Test (Neter and Wasserman, 1974). A two factor ANOVA was carried out with variety and morphological or growth trait as the two factors (this is referred to as the combined analysis). The varieties were also analyzed independently (Neter and Wasserman, 1974).

## RESULTS

### Biomass

The two varieties, analyzed separately, showed similar trends, with the seedlings from the two lower carbon dioxide levels lower in biomass than those from the two higher levels. Allocation patterns between roots and shoots showed no significant differences. The combined root/shoot ratios were 0.689, 0.672, 0.708, and 0.776 for +0ppm, +75ppm, +150ppm, and +300ppm respectively. Roots were the largest fraction of biomass, accounting for approximately 40% of the total dry weight for all treatments.

There was a statistical difference between treatments with respect to the dry weight of buds, but this was complicated by the number of buds produced in each treatment. For example, the Rocky Mountain variety produced 18, 21, 34, and 38 buds per plant for +0ppm, +75ppm, +150ppm, and

+300ppm respectively. The dry weights per bud for the Rocky Mountain variety were 34, 42, 34, and 72mg for +0ppm, +75ppm, +150ppm, and +300ppm.

Volume

The volumes of the stem segments in the Sierran variety showed similar trends to that of biomass with a statistical grouping of both the two lower and two higher carbon dioxide levels. In the Rocky Mountain variety and in the combined analysis only the volumes of the stem segments at +300ppm were greater than all other treatments. Total volume of the main stem as determined by the combined analysis is shown in Figure 1.

Analysis of percent change in volume indicated that the higher volume at +300ppm for the Rocky Mountain variety may have been in part due to a statistically larger initial volume. Percent change in volume of the seedlings at +300ppm was only statistically greater than those at +0ppm (rather than +0ppm, +75ppm, and +150ppm as indicated by the ending volume). The percent change in volume for the Sierran variety at +150ppm was greater in percent change than all other treatments, whereas at +300ppm the volume was not statistically different from those at either of the lower carbon dioxide levels (Figure 2). In the combined analysis, the seedlings at +150ppm were also statistically the largest value in percent change in volume (Figure 3).

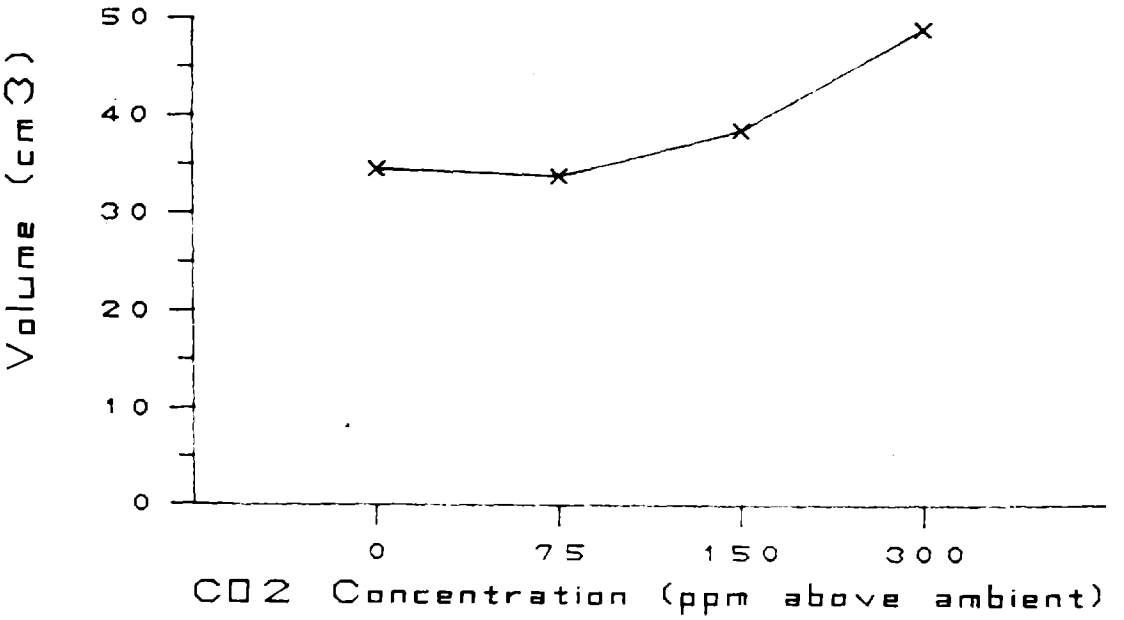


Figure 1.--Volume of the main stem at the various $CO_2$ treatment levels

Specific Gravity

Specific gravities, using the combined analysis, were 0.485, 0.529, 0.603, and 0.602g/cm$^3$ for +0ppm, +75ppm, +150ppm, and +300ppm treatments respectively. Statistically, only the seedlings at +150ppm and +300ppm were greater than those at +0ppm. The trend observed in specific gravity was due to variations in the Rocky Mountain variety.

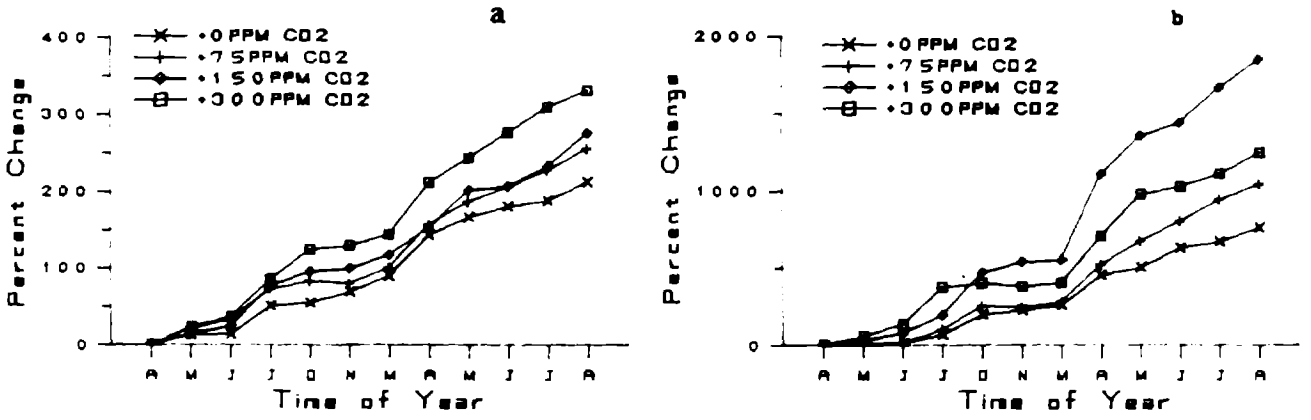


Figure 2.--Percent change in volume over the course of the study for a.) Rocky Mountain, and b.) Sierra.

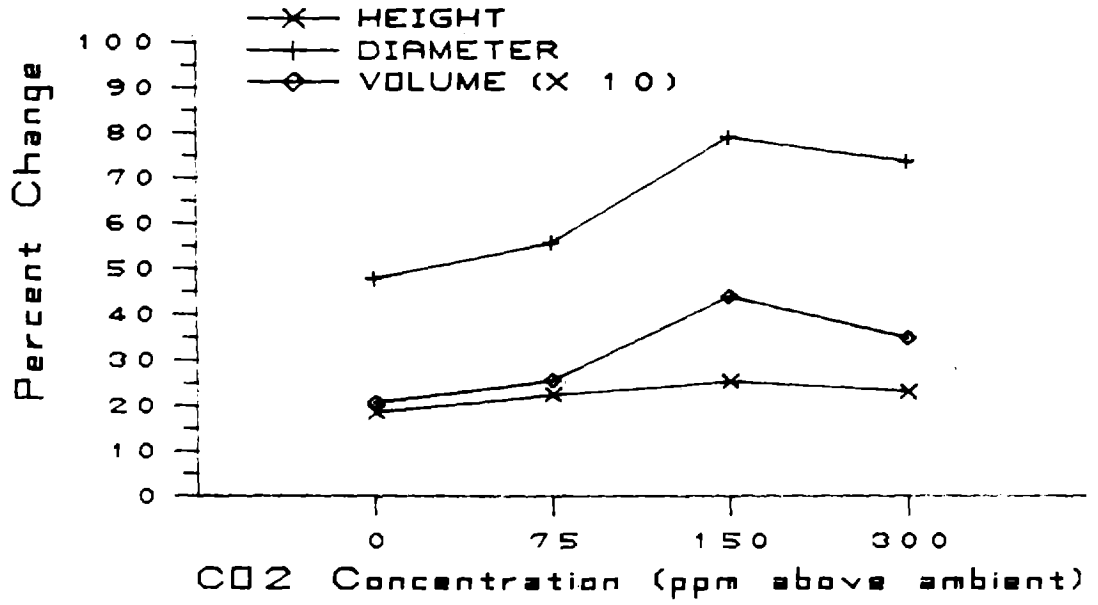


Figure 3.--Percent change in growth of height, diameter, and volume by the end of the experiment using the combined analysis.

Height

At the end of the study, the Sierran variety's seedling heights at +0ppm, +150ppm, and +300ppm were significantly greater than those at +75ppm. This was also true when applying the combined analysis. However, there were no significant differences between any of the treatments for the Rocky Mountain variety (Figure 4).

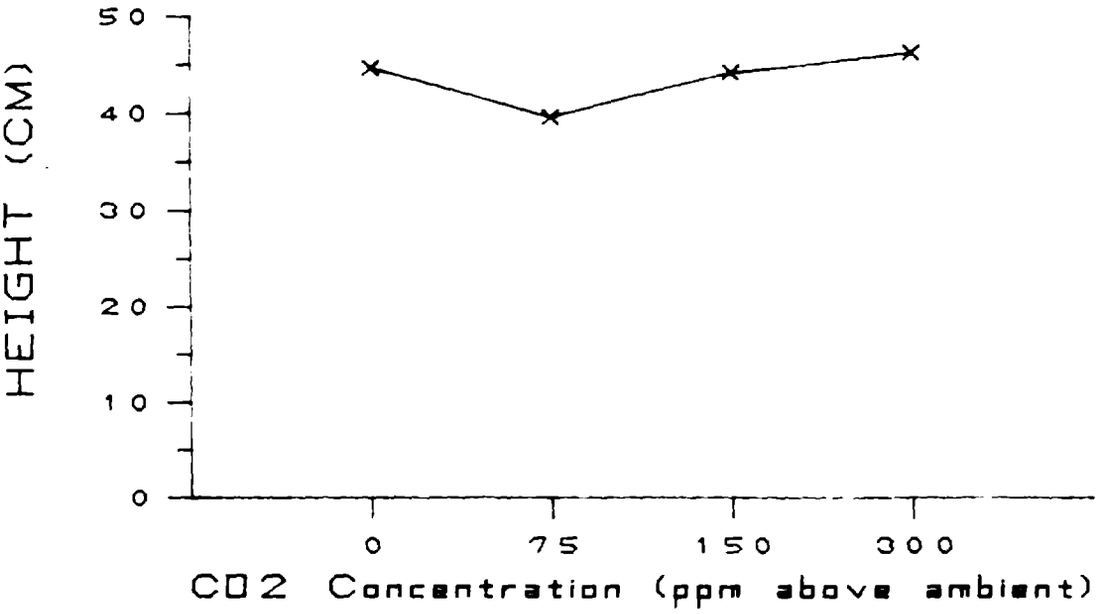


Figure 4.--Height from the cotyledon whorl to the tip of the apical bud for the seedlings in combined analysis.

In the independent analysis of total percent change of height for each variety, only the Sierran variety showed a significant difference (those at +150ppm were greater than those at +0ppm; Figure 5). However, using the combined analysis, the seedling heights at +75ppm, +150ppm, and +300ppm were significantly greater than those at +0ppm, and those at +150ppm were statistically greater than those at +75ppm and +300ppm (Figure 3). Thus, the differences observed in final height in absolute terms and with regard to the seedlings at +75ppm being lowest, can be attributed to a lower initial height.

Diameter

Diameter measurements were taken at each successive whorl up the main stem (Figure 6). In the combined analysis, the basal diameters of the seedlings at +0ppm and those at +75ppm were statistically less than those at +150ppm and +300ppm, and those at +150ppm were less than those at +300ppm. However, when comparing percent change of basal diameter, the seedlings at +150ppm were statistically the largest, followed by those at +300ppm, +75ppm, and +0ppm respectively (Figure 3). One reason for this difference was that the seedlings in the +300ppm treatment had a statistically larger initial basal diameter.

Needle Surface Area

The differences observed in surface area as determined by the combined statistical analysis were due to the Rocky Mountain variety. For the seedlings of the Sierran variety, the only significant difference in total surface area was that those at +300ppm were greater than those at +75ppm, and in the Rocky Mountain variety those at +150ppm were greater than those at +75ppm.

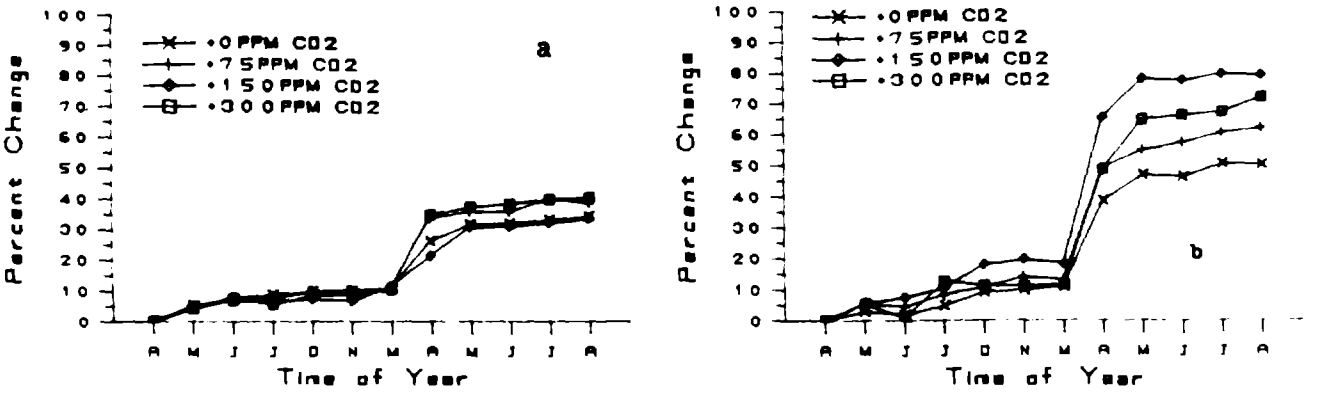


Figure 5.--Percent change in total height over the course of the study for a.) Rocky Mountain, and b.) Sierra.

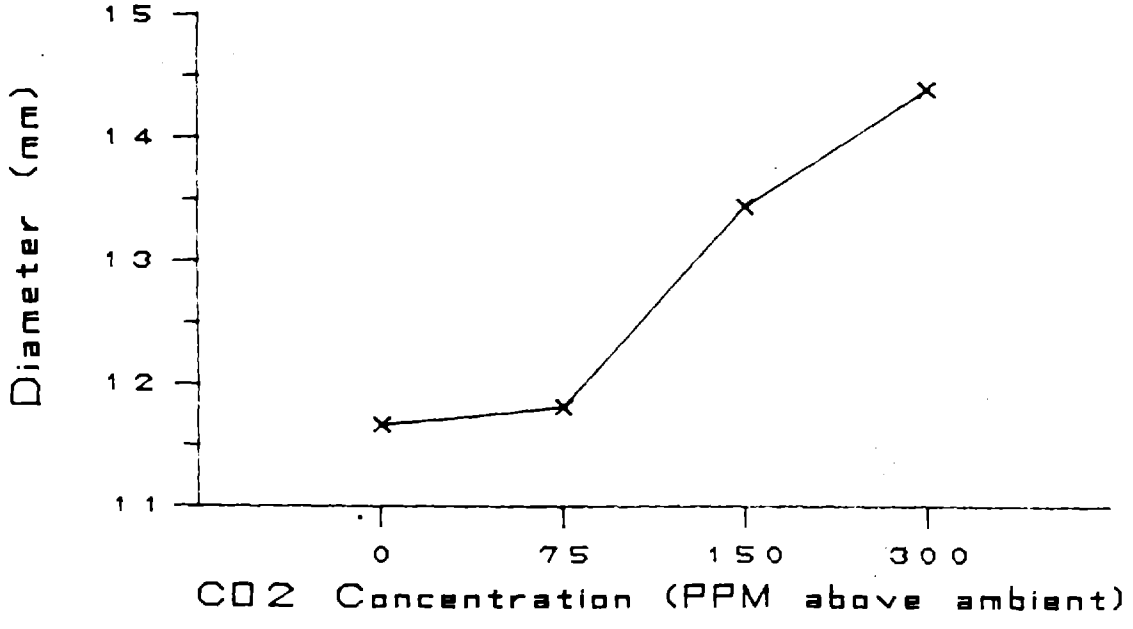


Figure 6.--Stem basal diameter for the combined analysis.

In Table 1 there are indications of a discontinuous phenomenon that occurred between +150ppm and +300ppm with respect to needle surface area. Mid-needle abscission was observed in the +300ppm treatment and this is partially responsible for the high standard deviation and large range for that treatment.

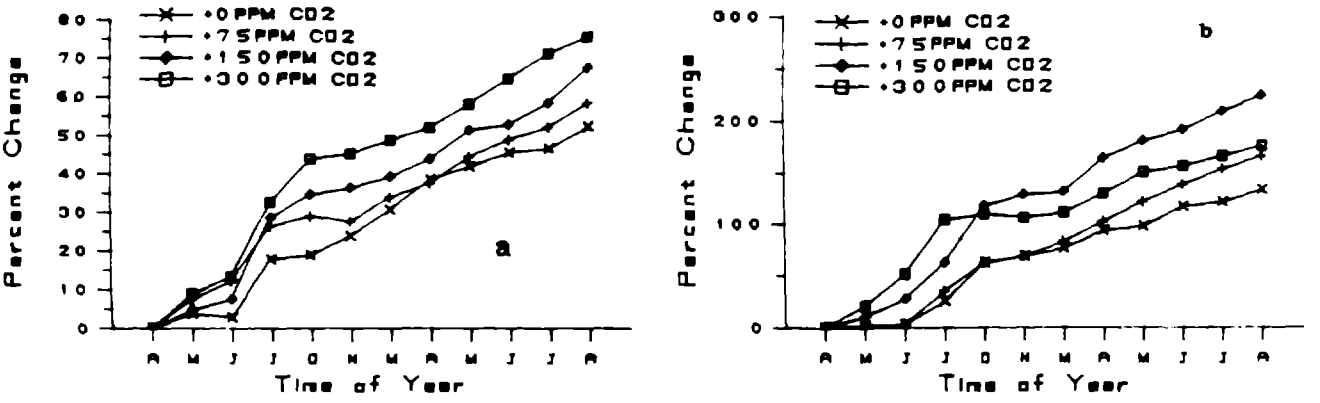


Figure 7.--Percent change in diameter over the course of the study for a.) Rocky Mountain, and b.) Sierra.

Table 1. -- Needle surface area for Sierran variety by carbon dioxide level.

| Carbon Dioxide Level (ppm) | Mean | Standard Deviation | Minimum | Maximum |
|---|---|---|---|---|
| +0 | 450 | 260 | 142.70 | 868.67 |
| +75 | 370 | 240 | 149.20 | 903.04 |
| +150 | 590 | 270 | 250.21 | 1062.71 |
| +300 | 770 | 590 | 47.57 | 1924.98 |

## DISCUSSION

Based upon absolute measures of morphology, there was the appearance of a beneficial effect of increasing carbon dioxide. Even though the seedlings were randomized at the start of the study, the seedlings at the +300 treatment were statistically larger in basal diameter and volume. Percent change is a more appropriate measurement because it eliminates the possible bias of initial size. Based upon percent change there were maximum benefits at +150ppm, with a reduction in growth at +300ppm. This was found in height, volume, and diameter growth. How other factors were affected by initial values, such as biomass and leaf surface area are unknown. Furthermore, the response to elevated carbon dioxide levels appears to be different between varieties of the same species. In particular, at +300ppm the Sierran variety had a reduction in percent growth, whereas the Rocky Mountain variety did not have a corresponding reduction.

## CONCLUSION

Although it is generally accepted that increasing carbon dioxide is beneficial to annual plants, it may be premature to extend this conclusion to naturally occurring long-lived plants such as ponderosa pine. This study indicates that there may actually be a detrimental effect beginning at concentrations greater than +150ppm. Such morphological evidence includes a decrease in percent growth and a reduction in needle surface area through mid-needle abscission. This study emphasizes the need for more long-term research on the effects of elevated carbon dioxide, particularly with respect to effects on long-lived woody perennial species and natural ecosystems.

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